nature reviews neuroscience

https://doi.org/10.1038/s41583-026-01047-z

Review article

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Neural basis of social hierarchy across species

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Abstract

A social hierarchy is an ordered ranking of individuals that arises through their interactions and governs relative access to resources and social influence. This form of social organization is pervasive across animal species and has a crucial role in shaping survival and reproductive outcomes. Across species, the routes to high status vary widely. As social groups become more complex, the basis of hierarchy shifts from simple residency rules to fighting-based dominance and finally to alliance-based systems. In this Review, we first examine the neuroendocrine and subcortical mechanisms that support status transitions in residency-based hierarchies. We then discuss plasticity within hypothalamic and mesolimbic circuits that underlie fighting-outcome-based social learning, through which fighting-based hierarchies emerge. Finally, we explore alliance-based hierarchies in cognitively complex species, in which individuals attain status through coalition formation, cooperation and reputation. We review evidence that cortical regions encode information about the strengths, emotions, experiences and intentions of other individuals and use this to navigate complex social interactions and attain status. As social hierarchies have shifted from primarily fighting-based to increasingly alliance-based strategies over evolutionary time, neural control of status has, thus, transitioned from subcortical social behaviour circuits to a more elaborated cortical network in humans.

Sections

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Introduction

Social hierarchy refers to the structured organization of individuals within a group, in which members differ in their influence and control over resources[1–3]. This form of organization is a fundamental feature of social life across species and has been documented in insects[4,5], fish[6–8], birds[9–11], rodents[12–14], non-human primates[15–17], humans[18,19] and many other species. Social hierarchies vary widely in form and steepness, ranging from despotic systems — in which a single individual monopolizes resources — to linear hierarchies, in which each group member occupies a distinct ranked position[20].

Within a hierarchy, the rank of an individual denotes its position in the overall structure and is conceptually analogous to an ordinal value on a number line[21]. By contrast, the terms dominant and subordinate describe relative positions between specific individuals[1]. In despotic systems, however, 'dominant' is often used informally to describe the highest-ranking individual, with all other individuals categorized as subordinates[1,20]. Dominant individuals typically benefit from priority access to food, mates and territory, exerting substantial influence over group dynamics, although this status can carry high energetic and survival costs in some species owing to high physiological demands[20,22–26]. Conversely, subordinates face restricted resource access and must strategically adapt their behaviour to minimize the risks of costly conflict[1,26].

Hierarchies emerge naturally in social groups because repeated interactions over limited resources require a stable mechanism for resolving competition[2,3]. Direct contests for food, shelter, mates or social support are energetically costly and risky, and hierarchies reduce these costs by establishing predictable asymmetries in access and influence[27]. Once ranks are settled, subordinates typically yield without escalation, thereby sharply reducing the frequency and severity of conflict[3]. Stable rank relationships also allow individuals to make decisions based on reliable expectations of competitive outcomes, reducing uncertainty in foraging and mating[28,29]. At the collective level, hierarchies enhance group cohesion and coordination by limiting unresolved conflict and enabling efficient division of labour or social roles[2]. Thus, across species, social hierarchies prevail because they increase efficiency, predictability and stability in social organization, ultimately improving survival and reproductive success.

The sex specificity of social hierarchies varies across species and reflects the ecological and reproductive pressures each sex faces. In some species, hierarchies form in both sexes, whereas in other species, they occur primarily in males or, less commonly, mainly in females[30] (Box 1). Dual-sex hierarchies arise when both sexes face meaningful competition over limited resources, such as food, nesting sites or social partners[30]. Male-only hierarchies occur in systems in which males experience intense sexual selection — often via competition for access to mating opportunities — whereas females face comparatively relaxed resource constraints[31]. Conversely, female-only hierarchies emerge when female reproductive success is constrained by access to critical resources, opportunities for cooperative breeding, or protection of offspring, generating strong competition among females but relatively weak competition among males[32] (Box 1).

In this Review, we first summarize the diverse routes through which stable social hierarchies arise across species, highlighting both fighting-based and non-fighting-based mechanisms. We then examine the neural and endocrine processes that support rapid status transitions in residency-based hierarchies. Next, we discuss plasticity within hypothalamic and mesolimbic circuits that underlie fighting-based dominance. Finally, we review the cortical networks that support social intelligence — a central determinant of high social status in humans.

Routes to high social status

Different routes to high social status in animals

The factors that determine social rank vary widely across species, yet in many animals, social hierarchies emerge through repeated agonistic encounters, during which individuals assess the competitive ability of one another using contest outcomes. This fighting-based mechanism is deeply conserved and has been documented across a broad range of taxa, from invertebrates to vertebrates[1,33]. Some examples include crayfish (*Procambarus clarkia*)[34], green anoles (*Anolis carolinensis*)[35], domestic fowl[36,37], mice (*Mus musculus*)[13,38], male elephant seals (*Mirounga leonine*)[39] and male chimpanzees (*Pan troglodytes schweinfurthii*)[40]. Together, studies of these species have demonstrated that competitive assessment through fighting is one of the most ancient and pervasive mechanisms underlying social rank.

Rodents provide a well-characterized mammalian model of fighting-based hierarchy formation. In most laboratory settings, male mice form steep, largely linear hierarchies through repeated offensive aggression, including biting, lunging and chasing[13]. Females, by contrast, typically display much milder forms of aggression — brief lunges, mounts, chases or threat gestures — and rarely escalate to sustained attacks[41]. Nevertheless, females still establish stable dominance relationships, although these hierarchies are generally less linear and less despotic than those observed in males[41]. Across sexes and species, once dominance relationships are established, the frequency of overt aggression declines sharply, as subordinates avoid challenging dominants and dominants reduce the need for costly enforcement[42]. This reduction in conflict is a general property of self-organizing hierarchies and serves to minimize energetic expenditure and injuries[26].

In many species, hierarchies do not exclusively rely on agonistic conflict. Social rank can also be influenced and, in some cases, determined through non-fighting-based mechanisms, including residency, alliance formation or, more rarely, seniority. In residency-based hierarchies, individuals gain dominance by securing valuable spatial resources, and intruders typically yield without escalation. This pattern is well documented in birds such as pied flycatchers (*Ficedula hypoleuca*), in which the existing residents of a territory reliably dominate challengers[43], and in teleost fish such as *Astatotilapia burtoni* and *Xiphophorus helleri*, in which prior residency strongly predicts dominance[44,45]. Residency-based systems remain flexible: when a dominant male *A. burtoni* vacates a territory, subordinates rapidly assume dominant colouration, behaviour and hormonal profiles upon territory acquisition[46]. Notably, both residency-based and fighting-based hierarchies can be context dependent. Although mice typically form fighting-based social hierarchies in laboratory settings, they establish and defend territories in more naturalistic environments when sufficient space is available[29,38,47]. In such contexts, conflict outcomes strongly favour territorial residents[29].

Alliance-based hierarchies arise when rank reflects patterns of social support rather than dyadic contest outcomes. These systems take both kin-based and non-kin-based forms. In kin-structured societies, such as female macaques and baboons, dominance is inherited matrilineally and maintained through nepotistic coalitions and grooming networks[48]. By contrast, non-kin alliance-based hierarchies are exemplified by male bottlenose dolphins, in which rank and reproductive success depend on the strength, stability and network structure of cooperative coalitions among largely unrelated males. Individuals embedded in stronger or more interconnected alliances gain greater access to females and sire more offspring, despite the absence of kinship ties[49,50]. Notably, fighting-based and alliance-based hierarchies often work together to determine social

status. In male chimpanzees, for example, whereas physical contests set initial rank, long-term dominance is stabilized by non-kin alliances: coalition partners provide support in conflicts and deter challengers[51,52]. Thus, coalition management can supplement or even substitute for direct physical competition in structuring dominance.

Tenure-based hierarchies, in which social rank is determined largely by length of residence within a group, appear far less common among non-human animals and typically operate only under specific social or ecological constraints[53,54]. The clearest example comes from male spotted hyenas, in which newly immigrated males enter at the bottom of the hierarchy and rise in rank strictly with length of residency, forming a queue-like structure that minimizes escalated aggression[54]. Collectively, these mechanisms — territorial occupancy, alliance formation and limited forms of seniority — demonstrate that hierarchies can be shaped by factors other than physical conflict in animals.

Different routes to high social status in humans

According to the seminal framework of Henrich and Gil-White[19], human social status — the widely shared recognition of an individual as competent, notable and worthy of influence — is attained through two primary

Box 1 | Sex differences in the expression of social hierarchies across species

Social hierarchies differ widely across species, and pronounced sex differences arise depending on how ecological constraints and reproductive pressures act on males and females. In many socially complex mammals, including macaques, baboons, chimpanzees, wolves, meerkats and laboratory rodents, both males and females form strong, independent dominance hierarchies because competition for limiting resources is present in both sexes. In primates, for example, males compete intensely for mating opportunities and establish rank through aggression, alliances and queuing (occupying a position in a social hierarchy and advancing sequentially to gain future access to rank or mating opportunities)[220,261], whereas females form stable, nepotistic, matrilineal hierarchies that regulate priority access to food, safe social partners and grooming networks[262]. These dual hierarchies persist because rank confers substantial fitness benefits to both sexes: high-ranking males gain increased reproductive success, whereas high-ranking females produce more surviving offspring and experience reduced physiological stress[178,261,263]. Similar patterns arise in social carnivores such as wolves and meerkats, in which dominant pairs monopolize breeding, but subordinate individuals of both sexes occupy well-defined positions within a cooperative hierarchy[264,265]. Even in rodents living in semi-natural arenas in laboratories, males and females each develop stable social hierarchies, through different mechanisms: males through aggression, chasing and territorial control, and females through approach–withdraw asymmetries, displacements and priority-of-access behaviours, despite minimal overt aggression[13,41].

Strongly male-biased and male-only hierarchies emerge when sexual selection and competition are high in males, whereas females experience weak resource or reproductive competition. Many lekking birds exemplify this pattern: males of species such as sage grouse and manakins engage in intense competition for display territories, forming steep, highly structured hierarchies in which dominant males obtain the majority of copulations[266,267]. Females, however, are largely solitary, do not defend resources against one another, and exhibit no stable dominance relationships. Similarly, in polygynous ungulates such as red deer, bighorn sheep and bison, males form strong seasonal hierarchies based on age, horn or antler size, and fighting ability to compete for breeding access[268–270], whereas females show weak or poorly defined dominance structures because they face minimal direct competition for mates or food under typical ecological conditions. An extreme example occurs in elephant seals, in which males establish hyper-aggressive, size-based rank orders that determine control of harems, whereas female–female dominance relationships are diffuse and not predictive of reproductive success[271]. Across these taxa, hierarchy is expressed primarily by males because male fitness is limited by mating opportunities, whereas female fitness is not improved by excluding other females.

A third pattern, found in fewer but well-studied taxa, is a strongly female-biased or female-only hierarchy, in which females form strong and stable dominance structures whereas males show weak or no hierarchy. This occurs when female reproductive success is strongly limited by access to key resources, such as breeding sites, helpers or nutritional support, whereas male reproductive competition is diffuse or based on alternative non-hierarchical strategies. Among marmosets, for example, a single dominant female typically monopolizes breeding and actively suppresses subordinate female reproduction via both behavioural intimidation and pheromone and endocrine mechanisms[272,273]. Males in these groups do not form linear hierarchies; instead, they participate cooperatively in infant care with little competitive structure. A similar pattern appears in naked mole-rats, in which the queen exerts strong behavioural and physiological dominance over all other females, establishing a strict reproductive hierarchy, whereas nonbreeding males show largely egalitarian, low-conflict relationships[274,275]. Female dominance is also characteristic of certain lemur species, such as ring-tailed lemurs, wherein females hold priority access to food and space and form stable linear hierarchies, whereas male rank is unstable, seasonal or weakly defined[276]. Even spotted hyenas show a form of female-centric social structure: female hierarchies are rigid, linear and nepotistic, whereas male rank largely reflects tenure rather than competitive ability[54,277].

Together, these three patterns indicate that the presence, strength and sex specificity of social hierarchies are not arbitrary species-level traits but predictable outcomes of the distinct selective pressures acting on males and females. Dual-sex hierarchies emerge when both sexes face meaningful, fitness-limiting competition — whether for mates, resources or social support. Male-only hierarchies arise when sexual selection generates intense male–male competition, whereas females gain little fitness benefit from excluding one another. Conversely, female-only hierarchies evolve in systems in which female reproductive success is tightly constrained by access to critical resources, helpers or safe breeding sites, and males adopt alternative strategies that do not require stable rank relationships. Across taxa, these divergent patterns demonstrate that social hierarchy is not a single universal structure but rather a flexible organizational solution shaped by ecological context, mating system, life-history strategy and cooperative demands.

pathways: dominance and prestige. Dominance-based status relies on coercion and resource control to elicit fear-based compliance, mirroring fighting-based hierarchies in animal societies. Although dominance can lead an individual to rapidly ascend a social hierarchy, it produces fragile, high-stress social status that collapses once the capacity for punishment wanes[19]. By contrast, prestige-based status emerges from perceived competence, typically derived from education, expertise or recognized achievement, and elicits voluntary deference grounded in respect[19]. Prestige parallels the tenure-based or residency-based systems seen in animals, in which prolonged experience leads to the accumulation of knowledge about the social and physical environment, rendering knowledge holders an advantage in conflict and making them valuable resources for the group.

However, in complex modern societies, prestige does not automatically translate into high social status. As Bourdieu[55] and Lin[56] have noted, prestige must be embedded within networks of relationships (alliances) or social capital. Here, alliances refer to structured, reciprocal social relationships that provide coalitionary support and help to stabilize and amplify the social standing of an individual. This necessity reflects the fundamentally collective nature of human status: rank is not merely claimed; it is conferred. These alliance networks act as a social infrastructure that amplifies and stabilizes reputational signals, mirroring the alliance-based hierarchies seen in animals, in which coalitional support sustains rank far beyond the isolated abilities of an individual. The integration of prestige and alliance facilitates the transition from informal respect to formal institutional authority. Modern organizations allocate high-status roles (such as executives or directors) through collective processes that treat prestige as a signal of competence and alliances as a signal of legitimacy. Once institutionalized, status becomes self-reinforcing; formal authority expands visibility and networks, making one's standing stable and portable — a phenomenon of cumulative advantage[57]. Thus, durable high status is the product of a prestige–alliance–institution cycle, in which accumulated competence is certified by collective endorsement and stabilized by structure.

Social capital, thus, serves as a crucial bridge between prestige and status[56]. Building this bridge requires social intelligence: the capacity to accurately perceive social cues, interpret and predict the intentions and emotions of other individuals, and flexibly adjust behaviours accordingly[58]. By integrating social perception with self-regulation, socially intelligent individuals are better positioned to form trust and sustain cooperative relationship more effectively[59]. Given this indispensable role, our discussion regarding alliance-based hierarchies centres on the neural substrates that mediate social intelligence.

Residency-based social hierarchy

In many avian and teleost species, social dominance is dictated by territorial ownership rather than intrinsic physical strength. This phenomenon is well documented in birds such as song sparrows, European robins and great tits, in which residents consistently defeat intruders regardless of size, and social rank shifts instantaneously if residency is experimentally manipulated[60–63]. A comparable residency-based hierarchy exists in teleost fishes, including African cichlids, angelfish, gobies and swordtails, wherein the acquisition of a territory is the primary prerequisite for dominant status[44,45,64,65]. In these species, subordinates typically adopt avoidant strategies to minimize direct conflict. Consequently, although dominance is maintained through agonistic interactions such as chasing and threat displays, escalation to high-risk physical fighting is uncommon; instead, control of the territory serves as the primary determinant of social rank.

The residency-based social hierarchy in teleosts is supported by hormone-mediated plasticity within the subcortical social behaviour network (SBN)[46,66,67]. The best-characterized example of this plasticity comes from the African cichlid *A. burtoni* (Fig. 1). These group-living fish form a male-specific hierarchy in which only around 10–30% of males are dominant territory holders, whereas the remainder become reproductively suppressed subordinates[44]. Dominant males occupy and defend territories, display bright colouration, and actively court and spawn with females; subordinates lack territories, exhibit dull colouration, and are not reproductively active[44]. Remarkably, when a dominant male is removed, owing to predation or by an experimenter, a subordinate male can rapidly switch to dominant colouration, occupy the vacated site, and begin defending it within minutes[68]. Sometimes, the vacant site will induce behavioural changes in multiple animals and aggressive competition among them[44,69]. The rapid physical and behavioural transitions are initiated within the central nervous system and are reinforced by swift activation of the hypothalamic–pituitary–gonadal axis[70]. Within 30 min of ascendion in rank, circulating sex steroid levels increase, and sex steroid receptors are upregulated in hypothalamic regions essential for aggression and reproduction[71]. Concomitantly, immediate early genes are strongly induced across nodes of the social behaviour network[72] in these ascending males, reflecting rapid neural plasticity that supports changes in social cue processing and the emergence of dominant behavioural phenotypes[68,71].

Conversely, when a dominant male is displaced by an intruder — typically a neighbouring dominant male or a size-matched challenger introduced experimentally — its bright colouration rapidly fades, it adopts subordinate behaviour within approximately 30 min, and plasma cortisol levels increase within 24 h[73]. Immediate early gene expression is also upregulated during the descending transition, but with spatial patterns distinct from those of ascending males. Whereas ascending males exhibit coordinated *cfos* and *egr-1* induction across multiple social behaviour network nuclei, descending males show more selective activation in regions such as the preoptic area (POA) and anterior tuberal nucleus, indicating that distinct transcriptional programmes underlie dominance acquisition and social suppression[74]. In stable social groups, dominant males maintain high testosterone levels to support reproduction, whereas testosterone in subordinate males remains chronically suppressed, with elevated cortisol and reduced reproductive capacity[66].

In residency-based hierarchies, steroid hormones coordinate social interactions by modulating the neural circuits underlying aggression, reproduction and social assessment, and by facilitating status recognition through hormonally driven changes in physical appearance[75]. Importantly, in *A. burtoni*, hormone levels and social status are not fixed or predetermined, unlike in eusocial insects such as honey bees and ants[76]. Instead, both endocrine state and social rank remain flexible and can shift rapidly in response to ecological conditions, particularly the availability and control of a territory. How the brain detects these environmental changes and initiates the behavioural and endocrine adjustments that precipitate transitions in social status remains poorly understood. This semi-flexible, residency-based, fighting-assisted, hormone-guided hierarchical organization helps to limit escalated intra-group conflict, structures access to resources and reproductive opportunities, and may support reproductive stability by maintaining a pool of replacement males[44,77].

Fighting-based social hierarchy

In most mammalian species, social hierarchies are established through agonistic dyadic interactions wherein the outcomes of fights determine

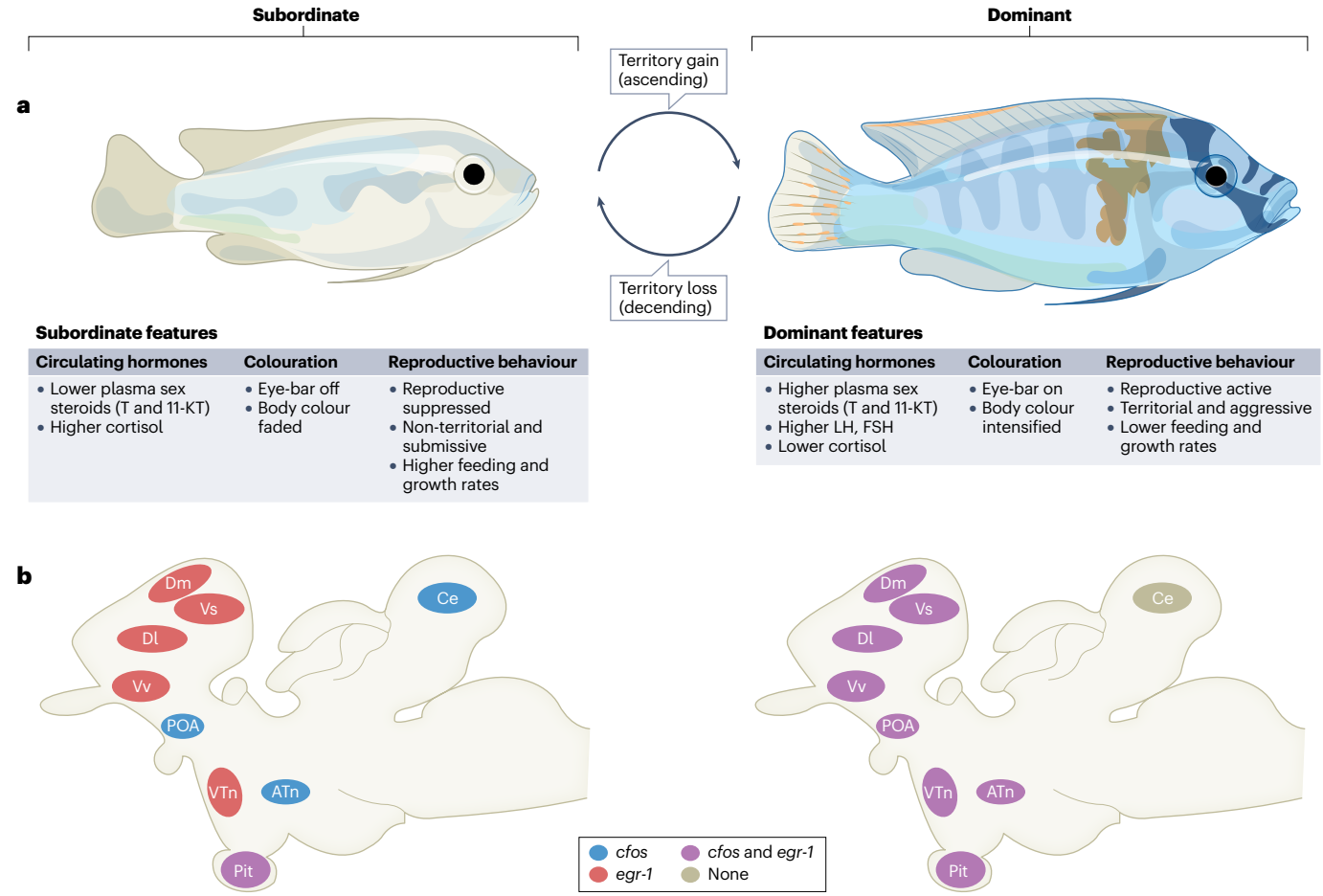

Fig. 1 | Rapid physical and neural changes during shifts in social status in African cichlid fish. a, When *Astatotilapia burtoni* individuals acquire or lose territory, they rapidly ascend or descend the social hierarchy. These shifts in social rank are associated with striking alterations in external appearance (coloration and morphology) and behaviour, as well as broad physiological hormone changes, reflecting the dynamic reorganization of status-related phenotypes[67,68,71]. **b**, Differential immediate early gene expression patterns in the brains of ascending and descending male *A. burtoni*. Ascending males exhibit uniformly elevated mRNA levels of both *cfos* (blue) and *egr-1* (pink) across all nuclei of the social behaviour network compared with stable-status controls[67,71]. By contrast, descending males show increased expression of either *egr-1* or *cfos* within individual nuclei, with the pituitary being the only region displaying elevated levels of both immediate early genes[74]. 11-KT, 11-ketotestosterone; ATn, anterior tuberal nucleus; Ce, corpus cerebellum; Dl, lateral zone of the dorsal telencephalon; Dm, medial zone of the dorsal telencephalon; FSH, follicle-stimulating hormone; LH, luteinizing hormone; Pit, pituitary; POA, preoptic area; T, testosterone; Vs, supracommissural nucleus of the ventral telencephalon; VTn, ventral tuberal nucleus; Vv, ventral nucleus of the ventral telencephalon. Part **b** adapted with permission from ref. 74, Company of Biologists.

dominance. Individuals with greater fighting capacity and motivation (that is, persistence in fighting) have higher tendency to win fights and attain dominant status[1,33]. The concept of a fighting-based 'pecking order' was first introduced by the Norwegian naturalist Schjelderup-Ebbe in 1922. Observing domestic fowl, he noted that aggression within a flock is largely unidirectional: the alpha individual pecks all other individuals, the beta individual pecks all but the alpha individual, and the lowest-ranking bird is pecked by every other member of the group[36]. Since then, fighting-based social hierarchy has been described in a wide range of species, including many laboratory rodents and non-human primates[13,14,78].

This form of social hierarchy formation can be conceptualized as a fighting-outcome-based social learning process. With each agonistic encounter, individuals update their assessment of their own fighting ability and adjust their willingness to engage in future conflicts. Winners exhibit a generalized increase in aggressive readiness that extends beyond the previous opponent to other conspecifics, a phenomenon known as the winner effect, whereas losers show a sustained suppression of motivation to escalate aggressive encounters[79,80]. Importantly, losers also learn to associate the cues of an opponent (conditioned stimulus) with the aversive experience of defeat (unconditioned stimulus), resulting in opponent-specific avoidance and reduced aggression during subsequent encounters[3,81–83]. Through repeated interactions with different group members, animals incrementally identify individuals with greater fighting ability and modify their behaviour accordingly, such as displaying submissive postures or retreating. These cumulative winner–loser effects and opponent-specific associative memories gradually give rise to stable, behaviourally recognizable

dominance–subordinate relationships within the group[3]. In some visually oriented species, learned dominance relationships are further stabilized by dynamic changes in external appearance that signal current status. For example, red junglefowl[84] and mandrills[85] alter ornamentation in ways that advertise dominance or submission, thereby facilitating rapid social assessment and reducing the likelihood of further escalation.

Role of social behaviour network

Recent studies in male mice have revealed the hypothalamic circuits that are crucial for fighting-outcome-based social learning in mice (Fig. 2). At the core of these circuits is the ventrolateral part of the ventromedial hypothalamus (VMHvl), which can be divided into anterior and posterior subdivisions. The posterior VMHvl (pVMHvl) is central for driving aggressive behaviours[86]. Cells within this region are activated during inter-male aggression[86]. Furthermore, experimental activation of these cells, especially those expressing oestrogen receptor (ESR1; pVMHvl^{ESR1} cells), promotes aggression, whereas inhibiting pVMHvl cells suppresses inter-male aggression[86–88]. pVMHvl cells undergo several forms of plasticity during repeated winning, resulting in increased pVMHvl responses to male conspecific cues. Specifically, when an animal wins once against a particular opponent, co-activation of the pVMHvl and posterior amygdala — a region that encodes sensory information about the opponent and provides excitatory input to the pVMHvl — induces Hebbian synaptic potentiation, leading to increased aggression selectively towards that defeated individual[80,89,90]. With repeated wins, pVMHvl^{ESR1} cells further increase their intrinsic excitability, resulting in a heightened readiness to attack any opponent and an increased probability of winning subsequent encounters[80] (Fig. 2).

In contrast to winning, social defeat suppresses aggression towards the victorious opponent. This process is supported by increased inhibition of pVMHvl^{ESR1} cells by ESR1-expressing neurons in the caudal medial preoptic area (cMPOA^{ESR1})[91] (Fig. 2). Under baseline conditions, cMPOA^{ESR1} cells are only weakly activated by male cues, but

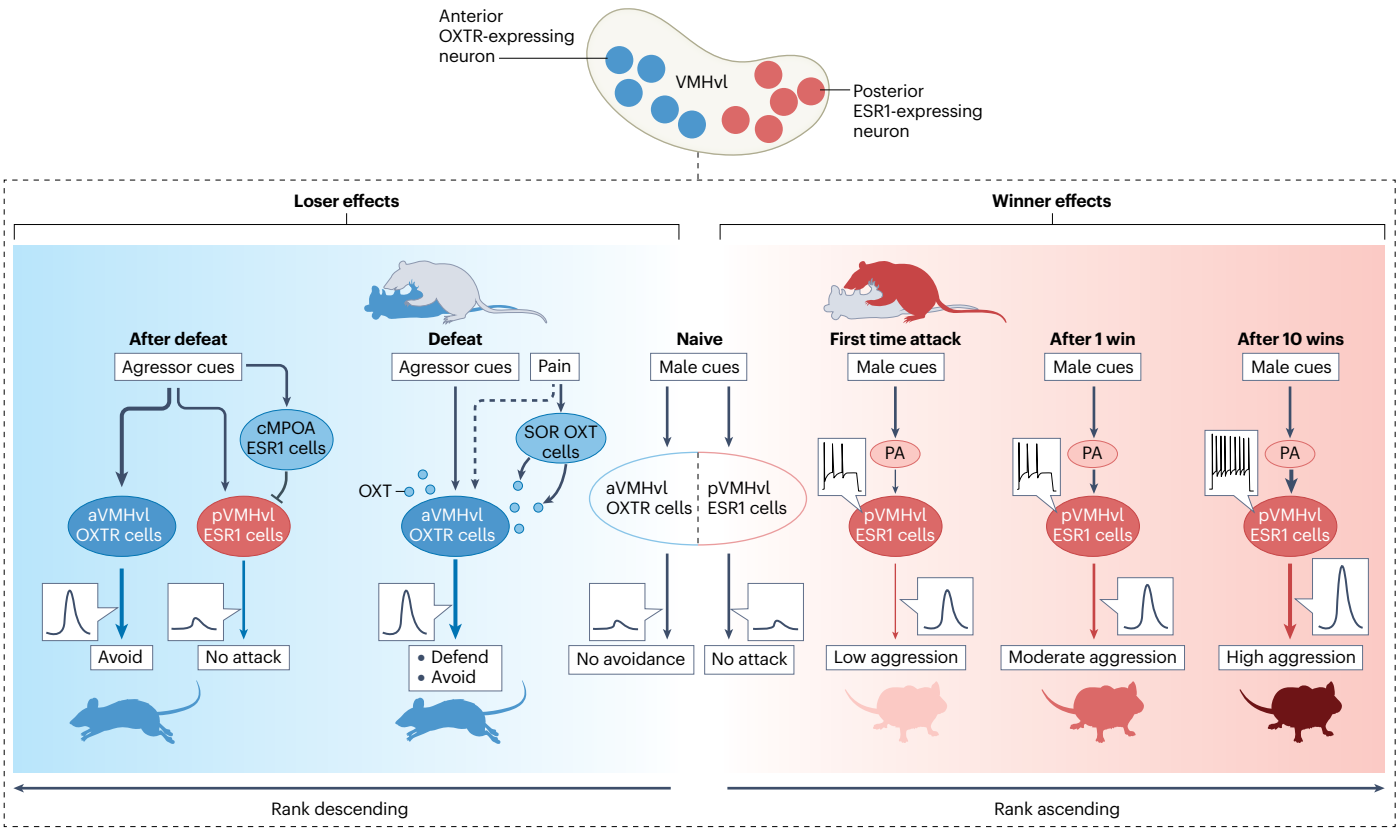

Fig. 2 | Hypothalamic circuits involved in fighting-based social hierarchy formation. Many mammals establish social rank through repeated agonistic interactions, with winner and loser effects encoded by distinct circuits centred in the ventrolateral part of the ventromedial hypothalamus (VMHvl). The neural mechanisms underlying behavioural adjustment after winning and losing in male mice are illustrated here. In naive, non-aggressive mice, the low activity of aVMHvl and pVMHvl neurons is insufficient to drive social avoidance or aggression. Repeated victories potentiate excitatory posterior amygdala (PA) inputs onto neurons in the posterior VMHvl (pVMHvl) that express the oestrogen receptor ESR1, increasing the excitability of these neurons and promoting winner-induced aggression and higher resource holding potential[80]. By contrast, social defeat engages anterior VMHvl (aVMHvl) neurons expressing the oxytocin receptor OXTR: during defeat, pain activates neurons in the retrochiasmatic supraoptic nucleus (SOR), promoting oxytocin release, which strengthens aggressor-responsive synapses onto aVMHvl^{OXTR} cells, driving avoidance of dominant conspecifics[83]. aVMHvl activation during defeat also promotes active social defence[92]. After defeat, caudal medial preoptic area (cMPOA) neurons expressing ESR1 are also recruited, which suppresses the activity of ESR1-expressing pVMHvl cells and, thereby, reduces aggression towards higher-ranking opponents[91]. Together, these synaptic and cellular adaptations bias animals towards aggression or avoidance in response to specific social cues, helping to establish stable social hierarchies. Traces next to the blue and red arrows indicate outputs of the indicated pathways. Traces next to the red ovals indicate cell excitability.

their responses to the winning opponent increase significantly and specifically after defeat. Because cMPOA^{ESR1} neurons strongly inhibit pVMHvl^{ESR1} cells, this defeat-induced increase in cMPOA^{ESR1} responses to aggressors suppresses pVMHvl^{ESR1} output and prevents further aggression towards superior opponents. Consistent with this circuit logic, inhibiting cMPOA^{ESR1} neurons results in increased aggression towards stronger opponents, triggering more attacks from the opponents and consequently more defeats[91].

Social defeat not only suppresses aggression but also induces social fear learning, enabling the loser to recognize and avoid the specific superior opponent in future encounters. Indeed, a single 10-min defeat is sufficient to cause a marked reduction in investigation of, and proximity to, the aggressor on the following day[83]. This form of opponent-specific fear learning is mediated in part by oxytocin receptor (OXTR)-expressing neurons in the anterior VMHvl (aVMHvl^{OXTR}), which are hardwired to drive avoidance behaviours, as evidenced by the immediate avoidance of a benign conspecific that is elicited by optogenetic activation of aVMHvl^{OXTR} cells in undefeated animals[83,92]. Before defeat, aVMHvl^{OXTR} neurons respond only weakly to male opponents. During defeat, noxious stimuli such as bites trigger oxytocin release from neurons in the retrochiasmatic supraoptic nucleus, located near the aVMHvl. The released oxytocin depolarizes aVMHvl^{OXTR} neurons and facilitates potentiation of the synapses carrying sensory information from the aggressor. As a result, cues associated with the aggressor, but not other male conspecifics, gain enhanced efficacy in activating aVMHvl^{OXTR} neurons, producing opponent-specific avoidance[83].

Notably, VMHvl neurons are unresponsive to non-social aversive or appetitive stimuli, such as predator odours or food scents[83]. Instead, these neurons are anatomically hardwired to receive social sensory information and engage motor programmes via downstream projections to premotor neurons in the midbrain[92,93]. Thus, the outcome of each agonistic interaction fine-tunes how the cues of an opponent are routed to avoidance-driving versus aggression-driving cells in the VMHvl, enabling differential behavioural responses towards different group members.

Similar plasticity tends to occur in other regions in the social behaviour network after winning and losing. For example, ventral premammillary nucleus cells show higher excitability in repeatedly winning male mice than in mice with no winning experience[94]. Cells in the posterodorsal part of the medial amygdala, conversely, show increased firing rates in repeatedly defeated rats that show social avoidance[95]. The lateral septum, a region that modulates aggression through its projection to the VMHvl, refines its local network after repeated winning[96–98]. Changes in individual nodes and their connections within this network collectively alter the input–output relationship of the aggression and social defence circuits, enabling the animal to adjust its tendency to confront or avoid an opponent

Sex hormones also have a role in some fighting-based hierarchies, in a manner that probably differs across species and contexts. In outbred CD1 mice, higher testosterone levels have been reported in dominant males compared with subordinates in highly despotic hierarchies, but testosterone levels are not correlated with social rank in more linearly organized social groups[99]. Consistent with this unsuppressed hormonal profile, subordinate males remain reproductively active despite their lower reproductive success[100]. It has been shown that an increase in testosterone is not a prerequisite for the circuit plasticity that leads to increased aggression in male mice[80]. However, in castrated mice with minimal testosterone levels, such plasticity is rarely induced, suggesting that testosterone has a permissive role in enabling aggression-related circuit modifications[89]. By contrast, in male *Peromyscus californicus*, commonly known as California mice, testosterone rises transiently after winning, and this increase is functionally important for the expression of the winner effect[101,102]. Together, these findings indicate that sex hormones interact with experience-dependent neural plasticity in species-specific ways, shaping how social hierarchies are learned and maintained.

Role of mesolimbic circuit

The canonical mesolimbic reinforcement learning circuit — centred on dopamine neurons in the ventral tegmental area (VTA) and their projections to the nucleus accumbens (NAc), basolateral amygdala (BLA) and medial prefrontal cortex (mPFC) — reinforces behaviours by using dopamine-dependent prediction-error signals to strengthen actions and cues that lead to rewarding outcomes[103]. In mice that are winning, dopamine release in the NAc increases[104], seemingly suggesting that a reinforcement learning mechanism contributes to the winner effect. However, depleting dopamine in the NAc does not block the rise in aggression after winning[98], indicating that the classic reward circuit does not directly 'reinforce' aggression itself. Likewise, no direct evidence supports a role for the BLA or mPFC in mediating the post-winning rise in aggression. Instead, elevated NAc dopamine during winning probably serves to associate preceding cues or instrumental actions with the rewarding outcome of victory. Supporting this interpretation, mice readily learn to lever-press or nose-poke to gain access to a weaker conspecific that guarantees an easy win and develop preferences for contexts associated with winning[105,106]. Inhibition of dopamine transmission or dopamine receptor D1 (D1R)-expressing cells in the NAc reduces lever pressing for access to the weak intruder[107,108].

In contrast to winning, strong evidence indicates that the broader mesolimbic learning network — including the VTA, NAc, tail of the striatum (TS), BLA, mPFC, lateral habenula (LHb), anterior bed nucleus of the stria terminalis (aBNST), and ventral hippocampus (vHip) — has a central role in defeat-induced social and contextual avoidance learning (Fig. 3). During defeat, dopamine release changes throughout the mesolimbic network. In the NAc, dopamine decreases when animals are attacked[104]. In mPFC, BLA and TS, dopamine either reportedly increases or is expected to increase (based on patterns observed during non-social fear conditioning)[109–112]. Regardless of the direction of change, the changes in dopamine signalling from the VTA act as a 'teaching' signal to promote plasticity within these regions during social defeat, thereby reshaping neuronal responses to aggressor cues and experience-associated contextual cues[113].

The changes in VTA dopamine neuron activity observed during defeat are at least in part due to changes in glutamatergic inputs from the LHb onto GABAergic neurons in the rostromedial tegmental nucleus (RMTg), which in turn exert strong inhibitory control over VTA dopamine neurons[114,115]. LHb neurons show marked increases in activity during acute defeat, and inhibiting LHb activity during defeat disrupts the subsequent development of social avoidance[116]. Beyond signalling the aversiveness of defeat, the LHb also encodes the negative valence of the aggressor after defeat. In defeated animals, LHb neurons exhibit robust responses upon encountering the aggressor, whereas naive animals show no such response[116]. These enhanced responses tend to reflect molecular, synaptic and physiological plasticity within the LHb. Although this has not been directly tested for social defeat, non-social chronic stress, such as repeated restraint stress and unpredictable daily mild stress, including overcrowding, cage shaking, bright light illumination and mild food deprivation, induces hyperexcitability of

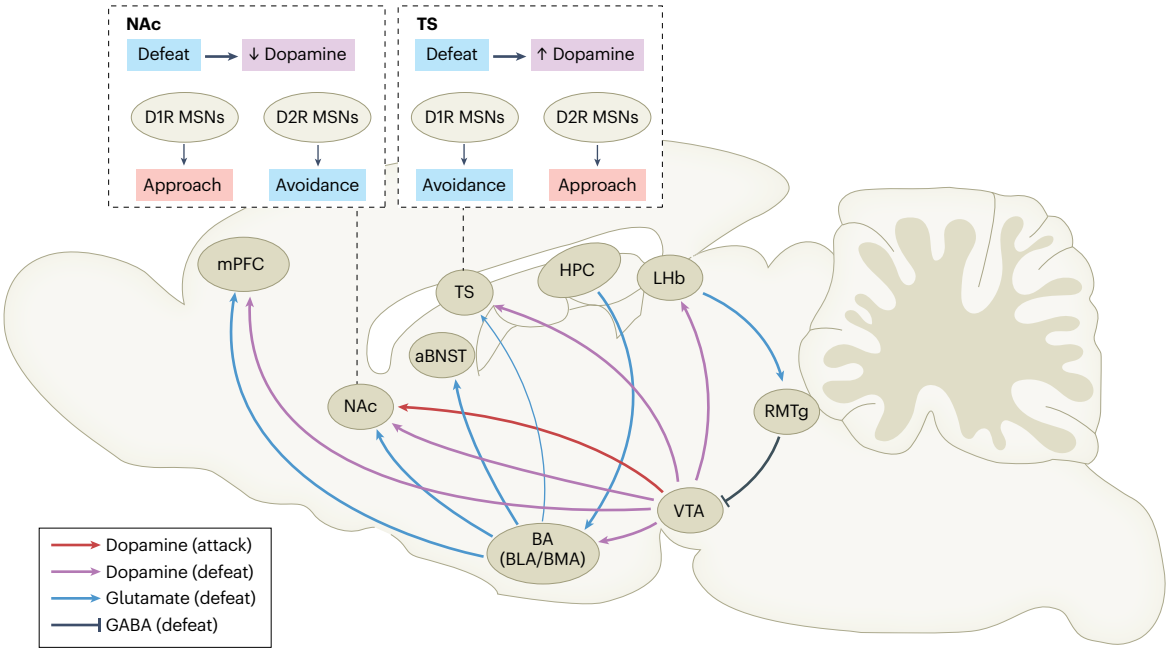

Fig. 3 | Mesolimbic circuit engagement during social winning and defeat. In mice, social winning, defined as successful overpowering of an intruder by the resident animal in a resident–intruder test, is accompanied by increased dopamine release by ventral tegmental area (VTA) neurons projecting to the nucleus accumbens (NAc)[104]. This dopamine signal reinforces actions and contexts associated with winning but does not directly drive aggressive behaviour itself[107]. By contrast, social defeat potentially recruits a broader mesolimbic and aversive-learning network that includes the VTA[104,112,260], lateral habenula (LHb)[116], basolateral amygdala (BLA)[123,125,126,128], medial prefrontal cortex (mPFC)[151], hippocampus (HPC)[126], anterior bed nucleus of the stria terminalis (aBNST)[136,139], nucleus accumbens (NAc)[104,112,143] and tail of the striatum (TS)[112]. During defeat, LHb-modulated VTA dopamine signals act as teaching signals that promote plasticity across these circuits, biasing behaviour away from approach and towards social avoidance and freezing following aversive experiences such as shock or social defeat[113,114,116]. BA, basal amygdala (comprising BLA and basomedial amygdala (BMA)); RMTg, rostromedial tegmental nucleus; D1R, dopamine D1 receptor-expressing neuron; D2R, dopamine D2 receptor-expressing neuron; MSN, medial spiny neuron.

LHb neurons, increasing their responsiveness to aversive stimuli[117,118]. After chronic defeat, VTA dopamine neurons show increased baseline excitability, spontaneous firing and burst activity[119], and this heightened activity correlates positively with social avoidance[120]. Thus, a combination of enhanced LHb responses to aggressors and elevated VTA baseline activity probably leads to changes in dopamine release during post-defeat aggressor encounters.

VTA dopamine neurons project densely to the BLA and have a critical role in gating BLA synaptic plasticity[121]. The BLA is well positioned to store negative representations of the aggressor — such as its odour or appearance — given its access to diverse sensory inputs and its established role in associating a conditioned stimulus with an aversive unconditioned stimulus[122]. Blocking BLA activity or plasticity during defeat impairs social avoidance learning in hamsters and mice[123–126], whereas enhancing cAMP response element-binding protein (CREB) signalling in the BLA increases avoidance following defeat[127]. Moreover, inhibiting the BLA immediately before post-defeat social interaction testing reduces avoidance[128], consistent with the idea that the BLA stores the negative valence of aggressor cues. Although direct recordings from the BLA are still lacking, defeat is expected to enhance BLA responses to dominant animals, analogous to the increased responses to shock-paired conditioned stimulus observed in classical fear conditioning[129,130].

Subordinate animals also learn to avoid territories occupied by dominant individuals, indicating robust contextual learning in addition to cue-based learning[13]. In mice, the vHip is a key site for encoding aversive contextual memories, as its inhibition reliably disrupts contextual fear learning[131,132]. During contextual fear conditioning, subsets of vHip neurons activated by shock undergo circuit reorganization that enhances synchrony upon re-exposure to the conditioned context[133]. vHip conveys contextual information directly to the basal amygdala, comprising both the BLA and basomedial amygdala. After aversive learning, synapses from context-activated vHip neurons onto basal amygdala neurons are strengthened[131]. Thus, when animals re-enter defeat-associated contexts, such as the territory of a dominant conspecific, BLA activity tends to be enhanced by strengthened and synchronized vHip inputs.

After defeat, aggressor-evoked responses in the BLA and VTA are expected to recruit downstream regions that mediate persistent social vigilance, reduced approach and enhanced avoidance. Three such regions — the aBNST, NAc and TS — are particularly well positioned to shape post-defeat behaviour. In humans, aBNST is known for its role in anxiety[134]. Consistent with this role, in hamsters, pharmacological inhibition of the aBNST at the time of testing using muscimol or corticotropin-releasing factor receptor antagonists reduces avoidance of a conspecific after defeat[135,136], whereas inhibiting the aBNST during defeat does not prevent the emergence of social avoidance 24 h later[136]. Similar anxiogenic effects have been observed following OXTR activation in the aBNST of female California mice[137,138], whereas genetic deletion of OXTR in the aBNST increases social approach[139]. The aBNST receives strong, topographically organized input from

the BLA, and selective activation of anterior BLA–aBNST projections promotes anxiety in male mice[140]. Together, these findings suggest that enhanced BLA responses after defeat recruit the aBNST to maintain a prolonged anxiety-like state that biases social encounters towards vigilance and withdrawal, even though defeat memory itself may not be stored within the aBNST.

The NAc receives dense input from the BLA and has a critical role in regulating approach behaviour[141]. Its principal neurons, the medium spiny neurons (MSNs), can be divided into D1R-expressing and D2R-expressing populations with opposing behavioural effects: D1R MSNs promote approach and reinforcement, whereas D2R MSNs suppress approach[142]. During defeat, reduced dopamine signalling in the NAc facilitates synaptic plasticity that weakens glutamatergic inputs onto D1R MSNs while strengthening inputs onto D2R MSNs[143], thereby biasing behaviour away from approach. Consistent with this model, optogenetic enhancement of NAc dopamine signalling during defeat attenuates subsequent social avoidance[104,112].

In contrast to the NAc, the TS promotes threat avoidance[144,145]. Dopamine signalling in the TS increases in response to threatening stimuli and promotes avoidance behaviour. As in the NAc, the TS contains D1R and D2R neurons, but their functional roles are reversed: D1R neurons promote avoidance, whereas D2R neurons suppress it[145]. Notably, VTA dopamine release in the TS increases dramatically when defeated animals approach an aggressor, and this response grows with repeated defeat episodes[112], supporting a role for the TS in reinforcing avoidance of social threats. Thus, defeat learning in mice appears to suppress approach by biasing D2R over D1R signalling in the NAc, while simultaneously promoting avoidance by biasing D1R over D2R signalling in the TS.

Finally, the mPFC receives strong inputs from both the BLA and VTA and has been implicated in social dominance in several recent studies, particularly those using competition-based tests[146,147]. However, such paradigms often do not align with fighting-based social hierarchies (Box 2). Nonetheless, substantial evidence supports an important role for the mPFC in active avoidance learning across social and non-social contexts[148–151]. Lesions or inhibition of the mPFC impairs the ability to switch from freezing to active escape in response to threat-predictive cues[148] and disrupts learning to avoid shock-paired conspecifics in social fear paradigms[151]. More broadly, mPFC dysfunction leads to deficits in behavioural flexibility during rule switching or changes in action–outcome contingencies[152]. In complex social groups, subordinate animals must continuously select actions that minimize conflict while securing access to resources based on social context, experience and internal state. The mPFC is, therefore, well suited to guide adaptive action selection — promoting appropriate avoidance while suppressing maladaptive responses — through its extensive projections to the striatum and amygdala[152].

Comparing male and female circuits

In house mice, fighting-based social hierarchies are less despotic and less linear in females than in males[41]. Several behavioural and circuit-level differences probably contribute to this sex divergence in social structure. First, aggression in virgin female mice is low and, crucially, does not increase following winning, which limits the escalation and intensity of fights among females[153]. In rodents, although lactating females display elevated aggression (known as maternal aggression), this increase is tightly coupled to the postpartum state rather than to winning experience[154]. Thus, in contrast to male aggression, female aggression is not strongly shaped by fight outcomes.

These behavioural differences are paralleled by sex differences in hypothalamic aggression circuits. A recent paper has reported that, in female mice, aggression-driving neurons in the pVMHvl are fewer in number, exhibit lower intrinsic excitability, and receive weaker excitatory synaptic input than those of males[155]. As a result, the circuit is less readily recruited and exhibits less plasticity in response to fighting experience. In addition, winning-induced dopamine release, a signal that supports associative learning, has been shown to be significantly smaller in females than in males[104], further constraining experience-dependent reinforcement. Consistent with this reduced dopaminergic engagement, females do not develop a preference for locations associated with winning[153]. Importantly, these sex differences in aggression circuitry may not be universal across species. In taxa with female-dominant hierarchies (Box 1), female aggression circuits are probably more active than those of males. Despite these sex differences in winning-related plasticity, both male and female mice readily learn to avoid aggressors after defeat[83]. This avoidance learning is supported by conserved hypothalamic social learning circuits. Specifically, aVMHvl^{OXTR} neurons in both sexes show increased responses to winners following defeat and causally drive social avoidance[83]. Whether quantitative sex differences exist in the strength, dynamics or plasticity of this circuit remains an important open question.

Several sex differences in mesolimbic circuit responses to stressful experience in mice have been identified. For example, increased firing of LHb neurons projecting to the VTA has been observed in females, but not males, following mild chronic stress[156]. Another study has found that subchronic stress selectively reduces spontaneous firing of VTA dopamine neurons in females, with no comparable effect in males[157]. In the NAc, females show higher expression of *Dnmt3a*, the gene encoding a DNA methyltransferase that is important for stress-induced epigenetic remodelling, than males after subchronic stress[158]. These circuit and molecular differences are accompanied by sex-specific behavioural and endocrine outcomes: females, but not males, show increased anxiety-like behaviour in the novelty-suppressed feeding task[156] and elevated circulating corticosterone levels following chronic mild stress[158]. Consistent with these findings, in California mice, a species in which both sexes display high levels of aggression, repeated social defeat induces social withdrawal[159] and suppresses aggression[160] in females but not males. These sex differences in behaviour are accompanied by differences in the molecular changes that occur in the VTA[161], paraventricular nucleus of the hypothalamus[160] and BNST[159]. Together, these findings indicate that mesolimbic circuits in females are more sensitive to stressful experience than those in males. Such heightened stress sensitivity could, in turn, promote faster behavioural adjustment after losing and reduce the likelihood of prolonged agonistic interactions among females by promoting withdrawal and conflict avoidance.

Summary

Social hierarchy formation reflects an iterative process of fight-outcome-dependent behavioural adjustment. In mice, winning-induced increases in aggression and losing-induced suppression of aggression are mediated primarily by plasticity within hypothalamic aggression circuits, with a minimal contribution from the canonical mesolimbic reinforcement learning system. By contrast, losing-induced social and contextual avoidance depends on both specialized hypothalamic social learning circuits and the general-purpose mesolimbic learning network. This asymmetric engagement of mesolimbic circuitry may reflect distinct computational demands: defeated animals must form precise memories of dominant individuals and their territories to

Box 2 | Studying hierarchies through competition tests

A commonly held view of social hierarchy posits the existence of a single underlying social order that regulates access to resources within a group[278]. According to this perspective, even in groups wherein overt aggression is rare, a 'hidden' hierarchy can be inferred from the order in which individuals access valued resources. Following this logic, laboratory tests based on resource competition have been used since the 1930s to infer dominance relationships[278]. In these paradigms, animals compete for access to a desirable resource, such as food, water or a safe area to avoid aversive stimuli, under conditions in which only one individual can obtain the resource at a time. Animals that consistently secure greater access are deemed dominant by the experimenter.

In addition to these resource-competition tests, a non-resource-competition test, the tube test, has gained particular popularity over the past 15 years[279,280]. In this task, two animals, typically mice, are released from opposite ends of a narrow, transparent tube and encounter one another in a 'passing' dilemma. Because the tube is too narrow for both animals to pass simultaneously, one individual must yield by retreating. The animal that forces its opponent to back out is designated the winner[280]. The tube test has been considered to measure competition over priority or 'right of way' rather than over a materialized resource. Multiple studies have shown that a stable rank order can be extracted within small groups of mice across repeated testing sessions[146,281]. Manipulations of mPFC activity, synaptic transmission or thalamic inputs can alter tube-test rank order, leading to the influential idea that the mPFC has a central role in regulating social hierarchy[146,281].

However, accumulating evidence indicates that hierarchies derived from competition tests are often uncorrelated with fighting-based social hierarchies, and that rankings can vary substantially across different competitive assays[278,282–284]. For example, a negative correlation has been reported between tube-test dominance and fighting-determined dominance in aggressive CD1 mice[282], consistent with earlier work showing that less aggressive animals often outperform more aggressive individuals in the tube test[285]. Mechanistically, this dissociation is not surprising. Pushing is the primary strategy used to win the tube test[281]. By contrast, during real fights, losers frequently use pushing defensively to fend off attacks, whereas winners typically rely on offensive behaviours, such as lunge and bite, and rarely push forward[286,287]. As a result, subordinate animals may actually be more proficient at the motor and postural strategies required to 'win' the tube test.

It has also been reported that there is no correlation between fighting-based social dominance and dominance in a food competition test in either C57 or CD1 mice[282]. Although this may initially seem counterintuitive, resource competition tests and fighting rely on fundamentally different abilities. In food competition tasks, individuals with faster reaction times, higher locomotor speed, superior spatial navigation or stronger motivation for food have higher tendency to succeed. Although physically dominant animals could, in principle, use aggression to displace competitors, direct interference competition is costly and, therefore, tends to be deployed selectively, most often when resources are highly valuable or defendable, such as salient territories[288]. Laboratory competition paradigms usually involve modest rewards delivered repeatedly in arenas that are difficult to monopolize. Under these conditions, working faster or more efficiently is more cost-effective than exerting dominance through force[289,290]. Thus, success in a resource competition test primarily reflects the ability of an animal to optimize performance under the specific constraints of that task. This ability is often unrelated to fighting capacity, which remains the primary determinant of social rank in freely interacting animal groups. Accordingly, it is unsurprising that rankings derived from competition tests frequently fail to predict naturally formed, fighting-based social dominance.

It is worth noting that although non-fighting-based 'winning' may arise mainly in human-designed laboratory paradigms for animals, humans themselves routinely engage in analogous activities — from sports to video games. Winning in such contexts reflects dominance within a narrowly defined rule set and skill domain, rather than general social dominance. Different individuals may dominate different competitions depending on their particular strengths, and no single, universal ranking spans all competitive domains. We, therefore, suggest that animal competition tests are best conceptualized as analogues of domain-specific human competitions, rather than as assays of general social hierarchy. Neural mechanisms that support superior performance in these animal tasks may nonetheless provide valuable insight into the circuits underlying human competitive behaviours that rely on similar cognitive, motivational or motor skills.

prevent future conflict, whereas winners do not necessarily need to discriminate among subordinates. Species-specific and sex-specific properties of aggression and learning circuits probably shape key features of social hierarchy, including its despotism and long-term stability.

Alliance-based social hierarchy

In many cognitively complex species, alliance-based social hierarchy emerges as a supplementary or alternative pathway to high social status. Rather than solely relying on individual competitive strength, individuals in these societies ascend the hierarchy by forming stable, strategically valuable partnerships that enhance their position in group-level conflicts. This coalitionary mechanism allows even physically modest individuals to attain elevated status through social support, as documented in male chimpanzees[51,162,163], bottlenose dolphins[164,165], spotted hyenas[166] and ravens[167]. Across these species, rank shifts often follow changes in coalition structure rather than changes in physical condition, underscoring that social power is constructed through cooperative relationships rather than fighting ability[163,168,169]. Notably, humans rely on alliance-based pathways to an exceptional degree, as social capital is often indispensable for converting individual expertise and accomplishment into institutional authority and widely recognized social status[19,55,56].

Success in alliance-based hierarchies depends on a suite of advanced social abilities — collectively termed social intelligence — that enable individuals to navigate complex relational landscapes[170]. Central to this is the capacity to accurately perceive social cues and use that information to guide decision-making[163,171]. This process is facilitated by social observational learning, which allows individuals

to understand the traits, social structures and action–outcome relationships of other individuals from third-party interactions without direct involvement[163,172,173]. In humans, this intelligence extends to theory of mind (ToM) — the capacity to infer the emotions, intentions and motivations of other individuals[174]. ToM enables individuals to not only interpret but also anticipate the responses of allies and rivals during cooperation and competition.

Social intelligence across species

From an evolutionary perspective, social intelligence is viewed as an adaptation to the challenges of group living and is shaped by the same selection pressures that act on physical traits[175,176]. The 'Machiavellian intelligence' and 'social brain' hypotheses propose that the cognitive demands of navigating complex group living — including strategic competition and alliance management, maintaining long-term social bonds, and tracking relationship information — favoured the evolution of expanded sociocognitive abilities, particularly in primates[176,177]. In species that live in stable, socially intricate groups, individuals with higher social intelligence are more successful in forming cooperative alliances, avoiding costly conflicts, securing resources and ultimately increasing their reproductive success[178,179]. Thus, the evolution of social intelligence reflects deep selective advantages conferred by skilful navigation in competitive and cooperative social environments.

Social intelligence can be conceptually divided into two levels. At the first level, individuals are aware of the identities, behaviour and emotional states of other individuals based on sensory cues and use this information to guide decision-making and learning. Many species that live in groups or alongside humans, including lemurs[180], monkeys[181], baboons[168], elephants[182], dolphins[183], spotted hyenas[184], dogs[185], ravens[186], rats[187] and mice[188,189], exhibit such social awareness and demonstrate social learning abilities. A recent preprint has reported on work in mice that illustrates this level of social intelligence in controlled experimental settings. In a foraging task designed to probe competitive decision-making, mice that perform the task alone reliably choose the higher-value reward option; however, in the presence of a competitor, especially one with high running speed, mice frequently choose a lower-value option that is spatially closer, reflecting strategic adjustment based on the position and capabilities of the competitor[188]. In another study reported in a recent preprint, pairs of mice were trained to obtain water rewards by simultaneously poking two ports within the same reward zone. Over weeks of training, a leader–follower relationship emerged, with the follower often waiting for the leader before committing to a choice[189]. Notably, such a leader–follower relationship does not always reflect the dominance–subordinate relationship. In cooperative lever-pulling tasks in marmosets, a species that lives in stable family groups, dyads improved coordination over time; strikingly, dominant individuals frequently attended to and followed the actions of the subordinate partner, consistent with a positive association between social intelligence and social status[190].

At the second level of social intelligence, individuals possess ToM — the capacity to recognize that other individuals possess internal mental states, such as beliefs, desires, intentions and emotions, that may differ from their own, and can attribute such states to both themselves and other individuals, as first formally articulated by Premack and Woodruff in 1978 (ref. 174). Advanced ToM enables more accurate inference of the needs and perspectives of other individuals, allowing individuals to anticipate the responses of other individuals, adjust their behaviour accordingly, and build and maintain social networks more effectively[191–193]. Compelling evidence for ToM remains strongest in humans. Although some studies suggest that non-human primates, particularly great apes, can track the goals, perceptions or knowledge of other individuals, whether they do so through attribution of mental states or through sensitivity to behavioural cues and learned associations remains unclear[194,195]. Whether non-human species possess ToM in the full human sense remains an open and actively debated question.

Neural mechanisms of social intelligence

The mPFC has emerged as a key region for social intelligence[196,197] (Table 1). Anatomically, it occupies the anterior portion of the frontal lobe along the medial wall. In rodents, the mPFC comprises the anterior cingulate cortex (ACC) and prelimbic and infralimbic cortices, with the ACC positioned dorsally and the infralimbic cortex ventrally. In primates, the mPFC spans the medial surface of the frontal lobe and is broadly subdivided into dorsomedial (dmPFC) and ventromedial (vmPFC) sectors. The ACC forms the innermost component of the mPFC, arching around the anterior corpus callosum; from dorsal to ventral, it can be further subdivided into dorsal, perigenual and subgenual regions (dACC, pgACC and sgACC), with the dACC generally associated with dmPFC and the pgACC and sgACC with vmPFC[198].

Notably, the rodent mPFC does not appear to contain direct homologues of all primate mPFC subregions. It is exclusively agranular,

Table 1 | Neural substrates supporting social intelligence across species

Social intelligence functions	Region	Species	Refs.
Monitoring the actions and status of other individuals	PL, ACC	Mouse	189,201–204
	mPFC	Monkey	205,206
	mPFC	Human	207
Encoding the reward of other individuals (versus oneself)	ACC	Monkey	208,209
	dmPFC, VTA	Monkey	210
	NAc	Rat	229
Encoding the emotional state of other individuals	ACC	Mice or rat	211,212
	ACC	Vole	213
	ACC	Human	214,215
Effort evaluation and decision-making	ACC	Rat	216,219
	ACC	Monkey	217,218
Observation learning	ACC	Mouse	222
	ACC-BLA	Mouse	223
	mPFC	Monkey	206
Mental-state inference (ToM)	dmPFC	Human	234,235,238,239, 241,246,247
	vmPFC	Human	251
	pSTS	Human	237,238,241
	TPJ	Human	238,239, 248–250,252,253

ACC, anterior cingulate cortex; BLA, basolateral amygdala; dmPFC dorsomedial prefrontal cortex; mPFC, medial prefrontal cortex; NAc, nucleus accumbens; PL, prelimbic cortex; pSTS, posterior superior temporal sulcus; ToM, theory of mind; TPJ, temporoparietal junction; vmPFC, ventromedial prefrontal cortex; VTA, ventral tegmental area.

lacking a well-developed layer IV, and has been proposed to be homologous primarily to the agranular components of the primate medial prefrontal cortex, specifically the ACC[198,199]. By contrast, the granular regions of the human mPFC, including Brodmann areas 9 and 10, appear to be absent in rodents. As a result, cognitive functions supported by granular prefrontal regions may be limited or difficult to model in rodents[200]. Nevertheless, across rodents, non-human primates and humans, neurons within mPFC encode rich 'other-oriented' information[196]. Below, we summarize these findings and specify relevant mPFC subregions whenever possible.

mPFC neurons signal information about the actions of other individuals, relative status (such as location and strength), and the outcomes of those actions. For example, in mice, some prelimbic cortex cells selectively increase activity during the behaviour of an opponent in both the tube test and free social interactions[201,202]. Similarly, during a food competition task, a subset of mPFC neurons in low-performing mice were excited when high-performing conspecifics succeeded in obtaining reward[203]. In a competitive foraging task, ACC cells adaptively represent the strength of an opponent relative to oneself, even before the start of competition[204]. Likewise, a recent preprint has reported that, in a social cooperation task, mPFC neurons encoded trial-by-trial leader–follower roles and represented an egocentric spatial map of the position of the partner. Inhibiting mPFC selectively impaired the ability of the follower to adjust behaviour on the basis of the location of the leader to maximize reward[189]. In non-human primates, many dmPFC cells were found to encode the actions of a partner monkey (such as whether they were pressing a green or yellow button) and the associated outcomes (reward or no reward)[205,206]. In humans, functional magnetic resonance imaging (fMRI) studies similarly revealed mPFC activation during observation of the decisions of other individuals[207]. Notably, the activation magnitude depended heavily on whether observers were required to infer the underlying intentions of the other individuals[207].

mPFC cells also encode rewards delivered to other individuals. Neurons in the monkey anterior cingulate gyrus (ACCg) were reported to signal reward outcomes delivered to oneself, to another individual, or to both[208]. This activity is functionally important: with an intact ACCg, monkeys learn cues associated with rewards delivered to their partners and often choose to provide such rewards rather than deliver nothing. By contrast, following ACC lesions, monkeys fail to learn cues associated with vicarious reinforcement[209]. Interestingly, mPFC responses are influenced by the relative distribution of rewards between self and other individuals. In one study in which the recorded monkey received a constant reward while the probability of the reward of its partner varied, dmPFC cells changed their spiking activity based on both self-reward and partner-reward amounts. Notably, when the reward probability of the partner increased, the recorded monkey devalued its upcoming self-reward, as reflected by reduced licking and changes in choice behaviours[210].

Beyond actions and outcomes, the mPFC, particularly the ACC, encodes the emotional states of other individuals. Single-cell calcium imaging and electrophysiological recordings in mice and rats show increased ACC activity when animals observe conspecifics experiencing pain (such as injury) or fear (such as that resulting from an unpredictable footshock)[211,212]. Functionally, inhibiting ACC neurons in mice reduces helping behaviours towards distressed conspecifics, such as allolicking, indicating its causal role in empathic responding[212]. Similarly, in prairie voles, ACC neurons exhibit markedly increased FOS expression when individuals observe their stressed partners[213]. Observing animals display anxiety-like behaviours, including self-grooming and freezing, which are abolished by local infusion of oxytocin receptor antagonists into the ACC[213]. In humans, observing other individuals in pain robustly activates the ACC and insula, often overlapping with regions engaged during firsthand pain experience[214,215]. Such shared activation patterns are widely considered a neural basis of empathy.

How does this wealth of other-oriented information help animals navigate complex social landscapes, including decisions about whom to ally with and whom to compete against? First, individuals use information about the strengths, intentions, past behaviour and social relationships of other individuals to estimate the probable costs and benefits of different actions. Such assessments can guide decisions on whether to engage in competition or to affiliate, cooperate and form alliances. Electrophysiological and perturbation studies in rodents (rats) and non-human primates (monkeys) implicate the ACC as a key site for such assessment. In non-social tasks, ACC neurons encode action–outcome associations and guide selection of strategies that maximize reward[216–218]. Disruption of ACC function impairs effort allocation towards optimal strategies[217,218]. Similarly, in social competition tasks, ACC incorporates information about the opponent into the calculations that guide actions. For example, in a competitive foraging paradigm in which rats choose between a small, uncontested reward and a larger reward requiring competition, ACC neuronal activity dynamically tracks the relative value of each option, and the choices of animals closely follow these neural signals. When rats can choose among different opponents, ACC neurons respond preferentially to weaker or less motivated competitors, biasing animals towards lower-cost contests[219]. Notably, accurate assessment of opponents and prediction of fighting outcomes can help animals faced with social conflict to select the right fight and avoid costly outcomes. Intriguingly, primates such as macaques rely more heavily on threat displays than on physical attacks to establish and maintain dominance–subordinate relationships[220] than rodents. This species difference may in part reflect the greater cognitive capacity of primates to evaluate social information. Such information may then be used to modulate attack initiation via projections from the mPFC to the periaqueductal grey, a key premotor region for the execution of aggressive behaviours[93,221].

Second, information about the experiences of other individuals supports observational learning. In chimpanzees, juveniles that closely observe social interactions, learning dominance relationships, alliance structures, and norms of coalitionary support form more effective alliances as adults, and this social knowledge strongly predicts later rank attainment[163]. Similarly, rhesus monkeys can learn dominance–subordinate relationships among other individuals by observing their interactions alone[173]. Recordings from macaque mPFC identified neurons that are activated by the erroneous actions of a partner in tasks wherein the observing monkey learned from the action–outcome contingencies of the partner to guide its own future decisions[206]. Rodents also exhibit observational learning. Mice can learn the aversive value of specific contexts or cues by observing a conspecific experience pain, for example, when footshocks are delivered in association with a predictive auditory cue. Inactivation of the ACC or its inputs from the parafascicular or mediodorsal thalamic nuclei severely impairs this form of learning[222]. At the output level, the ACC transmits information about the aversive experiences of other individuals to the BLA, wherein it can function as an unconditioned stimulus to support associative learning[223]. Because direct experience is limited and costly, learning from other individuals dramatically

expands the knowledge of an individual about the social and physical environment.

Third, the ability to compare one's own effort and reward with that of other individuals is fundamental to cooperation. Sustained cooperation among unrelated individuals requires mechanisms that ensure proportionality between contribution and pay-off, that is, fairness[224]. When pay-off disparities become excessive, disadvantaged individuals often respond with negative affect and withdraw from cooperative interactions, a phenomenon known as inequality aversion[225–227]. Accordingly, leaders who consistently demonstrate fairness, particularly in their treatment of followers, are evaluated as more trustworthy and effective, thereby linking fairness to elevated social status[228]. As noted above, the mPFC in monkeys encodes the rewards of other individuals relative to their own rewards[210], allowing detection of reward inequality. In rats, observing another animal repeatedly receive rewards suppresses dopamine release in the ventral striatum and elicits stress-related vocalizations in the observer, whereas identical reward delivery to an empty box does not. This dissociation indicates that perceived social inequality, rather than simple reward omission, drives the aversive response[229]. Together, these findings suggest that inequality signals computed in the mPFC engage mesolimbic dopamine circuits, suppressing ventral striatal dopamine and generating an aversive affective state.

Last, in humans, observable other-oriented information can be leveraged to infer the mental states of other individuals and predict future behaviour. Individuals with superior ToM abilities navigate social interactions more effectively and have higher tendency to attain influential positions. For example, developmental studies show that children with stronger ToM skills are rated as more socially competent and have higher tendency to emerge as leaders[230], whereas adult leadership research identifies perspective-taking and accurate inference of the intentions of other individuals as key predictors of leadership effectiveness[231,232]. Neuroimaging studies consistently show that the mPFC, particularly dmPFC regions (Brodmann areas 8, 9 and 10), is recruited during mental-state inference tasks, regardless of whether the 'other' is represented by geometric shapes, cartoons or narrative protagonists[233–237]. During strategic games such as rock–paper–scissors, mPFC activity increases when participants believe they are competing against another human and attempt to model the strategy of that opponent, even when the opponent is actually a computer[238,239].

In addition to mPFC, posterior cortical regions, including the temporoparietal junction (TPJ) and posterior superior temporal sulcus (pSTS), are consistently engaged during mental-state reasoning in humans[240–242]. The pSTS is particularly involved in processing biological motion and dynamic facial expressions[243], whereas TPJ integrates this information to generate model-based predictions of the mental states and actions of other individuals, which are then communicated to mPFC[244,245]. Consistent with the imaging results, lesions to the frontal cortex or TPJ impair sophisticated social reasoning[246–248], and transient disruption of TPJ or mPFC using transcranial magnetic stimulation or transcranial direct current stimulation similarly impairs mental-state inference[249–252]. Conversely, increasing dmPFC excitability using high-definition transcranial direct current stimulation enhances 'mind-reading' ability[253].

Notably, both mPFC and TPJ–pSTS are among the most expanded cortical regions in humans relative to macaques[243,254]. In fact, a strict one-to-one homologue of the human TPJ may not exist in non-human primates[243]. Together, these findings identify the mPFC and TPJ–pSTS network as a core substrate for ToM, although important questions regarding the precise computations and interactions within this system remain open.

Across species, social intelligence enables individuals to monitor the actions, status, relationships, emotions and outcomes of other individuals and to use this information to choose when to compete, when to cooperate and with whom to align. The mPFC, together with connected cortical and subcortical circuits, appears central to these computations, supporting strategic assessment, observational learning, sensitivity to fairness and, in humans, mental-state inference (Table 1). These processes are all highly relevant to alliance formation because successful coalitions require accurate evaluation of partner quality, prediction of the behaviour of other individuals, flexible adjustment to shifting relationships, and avoidance of costly or unstable social commitments. Thus, alliance-based hierarchies can be viewed as an emergent product of advanced social intelligence: the more effectively individuals infer, learn from and strategically respond to other individuals, the more successfully they can form alliances and convert social relationships into durable influence and status.

Concluding remarks

Social hierarchy is a fundamental and widespread social structure in which individuals occupy different ranks, tiers or classes. High social

Glossary

Hebbian synaptic potentiation
An activity-dependent increase in synaptic strength that occurs when presynaptic input repeatedly coincides with postsynaptic activity, often summarized as "cells that fire together wire together."

Reinforcement learning
A trial-and-error learning process in which behaviour is shaped by rewards and punishments, such that actions that lead to favourable outcomes become more likely, whereas actions that lead to unfavourable outcomes become less likely.

Sexual selection
An evolutionary process in which traits are favoured owing to their effects on reproductive success through mate choice or competition within a sex.

Social behaviour network
(SBN). A conserved set of highly interconnected brain regions, including the extended medial amygdala, hypothalamic nuclei and midbrain regions, which regulate core social behaviours such as aggression, mating and parenting.

Social capital
A set of resources that are accessible through social relationships and networks, shaped by trust, reciprocity and social structure.

Social intelligence
The ability to perceive, understand and flexibly respond to social cues, including inferring the identities, intentions and emotional or mental states of other individuals, to navigate and maintain social relationships.

Social learning
An experience-dependent process in which individuals change their behaviour or internal representations on the basis of information acquired from other individuals through direct interaction or observation.

Social vigilance
A state of enhanced attention to social cues and conspecific behaviour that supports rapid detection of threat, opportunity or changes in social context.

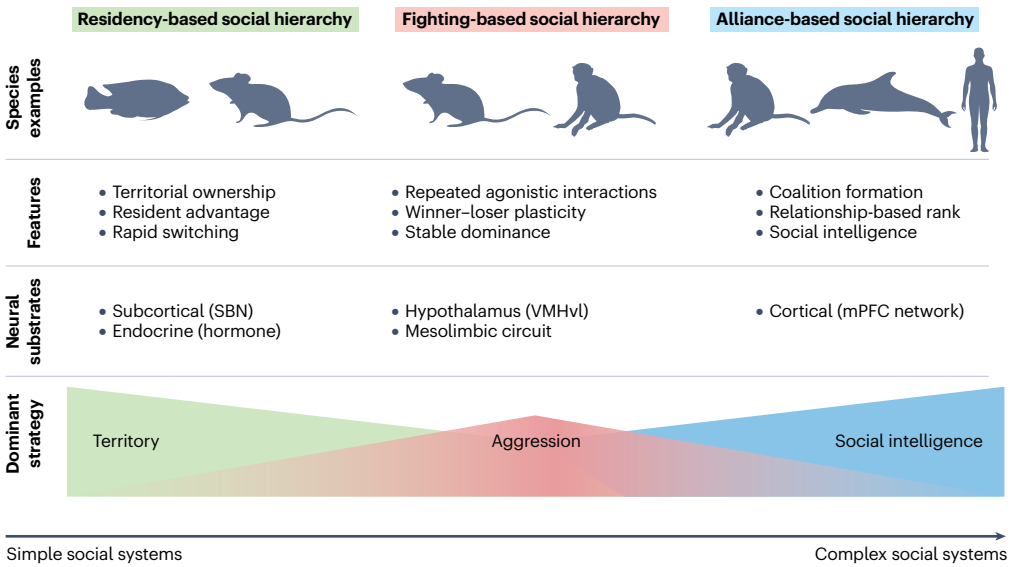

Fig. 4 | Evolutionary and neural organization of social hierarchy mechanisms. Social hierarchies arise through three major, partially overlapping mechanisms: residency-based, fighting-based and alliance-based strategies. In residency-based hierarchies, rank is determined by territorial ownership, with residents typically prevailing over intruders and status shifting rapidly as territory availability changes[44,45,60–64]. This form of hierarchy is supported primarily by subcortical social behaviour network (SBN) and endocrine regulation[46,66,70–72,74]. In fighting-based hierarchies, rank emerges through repeated agonistic interactions, during which winner-dependent and loser-dependent plasticity progressively biases animals towards aggression or avoidance, ultimately stabilizing dominance relationships[1,33,79–81]. These processes are mediated by hypothalamic circuits, including the ventrolateral part of the ventromedial hypothalamus (VMHvl)[80,83,86,89,91], together with a broader mesolimbic network[103,104,109–112]. In alliance-based hierarchies, rank is shaped by coalition formation and social relationships, relying on strategic cooperation and social intelligence supported by cortical networks centred on the medial prefrontal cortex (mPFC)[51,163–169,196,197]. Across evolution, as social systems increase in complexity and group size, there is a broad shift from territory-based and aggression-based strategies to alliance-based strategies, accompanied by a transition from predominantly subcortical to more cortical control[176,177]. These mechanisms are not mutually exclusive, and many species combine multiple strategies to determine social rank.

status confers priority access to resources and greater influence within the group, making it highly desirable in most cases, despite the high energetic and survival costs in some species[22–25]. Across species, the factors determining the social status of an individual vary widely (Fig. 4). In eusocial insects, for example, social class is rigid and primarily determined by genetic and environmental factors during development[76]. In *A. burtoni*, social status is dynamically regulated mainly by a single variable, territory. In most animal species, however, social hierarchies are established through agonistic interactions. From each fight, individuals learn to avoid conflict with those possessing superior fighting ability. This outcome-based learning is supported by plasticity in both hypothalamic social behaviour circuits and mesolimbic reinforcement learning circuits.

In modern humans, aggression has a minimal role in attaining social dominance. Instead, social status is achieved via a prestige–alliance–institution cycle, in which social intelligence is central to building alliance networks that enable the conversion of individual prestige into institutionally certified status. The mPFC serves as the core region for encoding diverse other-oriented information, which is then transmitted to downstream brain regions to guide decision-making, observational learning and judgments of fairness. With the support of an expanded mPFC and TPJ, humans also possess the capacity to infer the mental states of other individuals and anticipate their behaviours. This ability underlies complex social interactions, communication and cooperation that surpass those of other species. Individuals with high social intelligence can accurately infer the thoughts, beliefs and intentions of other individuals and adapt their behaviour accordingly to build strong relationships. Consequently, they have higher tendency to convert prestige into formalized institutional status[56] and to function as effective leaders[231,255].

In species that live largely solitary lives or in large, fluid groups, individuals obtain resources independently, and fighting remains the main mode of competition[1]. By contrast, in animals that live in small or moderately sized groups with stable membership, social hierarchies have increasingly shifted from being primarily fighting-based to alliance-based, as coalition formation and cooperative relationships become more important than individual physical strength for attaining high status[19,163,256]. This shift favours the reproductive success of individuals that are skilled at navigating complex social interactions to form and maintain alliances, thereby driving the evolutionary elaboration of social intelligence over generations. In early humans, hunting was the primary means of obtaining high-value nutrients, which required collaboration and resource sharing, further accelerating the evolution of social intelligence[257]. In modern humans, physical aggression is largely discouraged, whereas cooperation, from sharing household responsibilities to collaborating with colleagues, has become a fundamental part of daily life. As the means of attaining social dominance shifted over evolutionary time, the neural circuits supporting social-status success also expanded, transitioning from a hypothalamus-centred social behaviour network in non-human mammals to a more elaborated mPFC-centred cortical network in humans[258,259] (Fig. 4).

Published online: 14 May 2026

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Acknowledgements
The authors thank the Vulnerable Brain Project (D.L.), Brain Research Foundation (D.L.), and Brain and Behaviour Research Foundation (R.Y.) for support. ChatGPT 5.2 (OpenAI) and Gemini 3 (Google) were used to improve the structure and readability of the text and to suggest potentially relevant references for further evaluation. The references recommended by these tools were verified by the authors, who made the final citation choices. All scientific judgements and interpretations were made by the authors.

Author contributions
D.L. conceived the overall framework and scope of the review. D.L. and R.Y. co-wrote the manuscript. R.Y. prepared the figures.

Competing interests
The authors declare no competing interests.

Additional information
Peer review information *Nature Reviews Neuroscience* thanks Kay Tye, who co-reviewed with Christopher Lee; Steve Chang; and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.